

Galling by *Rhopalomyia solidaginis* alters *Solidago altissima* architecture and litter nutrient dynamics in an old-field ecosystem

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Abstract Plant–insect interactions can alter ecosystem processes, especially if the insects modify plant architecture, quality, or the quantity of leaf litter inputs. In this study, we investigated the interactions between the rosette gall midge *Rhopalomyia solidaginis* and tall goldenrod, *Solidago altissima*, to quantify the degree to which the midge alters plant architecture and how the galls affect rates of litter decomposition and nutrient release in an old-field ecosystem. *R. solidaginis* commonly leads to the formation of a distinct apical rosette gall on *S. altissima* and approximately 15% of the ramets in a *S. altissima* patch were galled (range: 3–34%). Aboveground biomass of galled ramets was 60% higher and the leaf area density was four times greater on galled leaf tissue relative to the portions of the plant that were not affected by the gall. Overall decomposition rate constants did not differ between galled and ungalled

leaf litter. However, leaf-litter mass loss was lower in galled litter relative to ungalled litter, which was likely driven by modest differences in initial litter chemistry; this effect diminished after 12 weeks of decomposition in the field. The proportion of N remaining was always higher in galled litter than in ungalled litter at each collection date indicating differential release of nitrogen in galled leaf litter. Several studies have shown that plant–insect interactions on woody species can alter ecosystem processes by affecting the quality or quantity of litter inputs. Our results illustrate how plant–insect interactions in an herbaceous species can affect ecosystem processes by altering the quality and quantity of litter inputs. Given that *S. altissima* dominates fields and that *R. solidaginis* galls are highly abundant throughout eastern North America, these interactions are likely to be important for both the structure and function of old-field ecosystems.

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Introduction

Interactions between insects and their host plants can alter the structure of communities as well as the functioning of ecosystems (Schowalter 2000; Hunter 2001). For example, even in non-outbreak years,

insect herbivores can directly alter terrestrial ecosystems by removing 10–20% of the aboveground biomass (Cyr and Pace 1993; Schowalter 2000). They can also affect ecosystem processes indirectly by altering the quality or amount of leaf-litter inputs (e.g., Chapman et al. 2003; Schweitzer et al. 2005), or by altering plant architecture (Martinsen et al. 2000; Lill and Marquis 2003; Classen et al. 2005). Any of these indirect effects of insects can influence leaf-litter decomposition rates and nutrient release patterns (e.g., Hunter 2001; Classen et al. 2007).

Gall-forming insects, as habitat modifiers or ecosystem engineers, may have especially strong ecological effects (Jones et al. 1997; Crawford et al. 2007). This is because galls persist on plants for long periods of time (often the whole growing season), may greatly alter plant architecture (Abrahamson and McCrea 1986; Fay and Throop 2005), induce changes in plant chemical quality (Abrahamson 1991; Hartley 1998; Nyman and Julkunen-Tiitto 2000; Allison and Schultz 2005), and alter the abundance of the associated arthropod community (Dickson and Whitham 1996; Martinsen et al. 2000; Crawford et al. 2007). For example, multiple studies across diverse plant and gall-former systems have found that galls serve as habitat for many other species of inquilines, including insects, spiders, and fungi (Weis et al. 1983; Martinsen et al. 2000; Hayward and Stone 2005; Crawford et al. 2007). In addition to altering communities, galling can cause changes in leaf architecture and litter quality that may have important afterlife effects on leaf-litter decomposition and nutrient release (Hunter 2001; Schweitzer et al. 2005). For example, Schweitzer et al. (2005) found that galling by *Pemphigus betae* reduced leaf litter quality and thus decreased decomposition rates: galled litter decomposed 40% more slowly than did ungalled litter. Galling can also decrease litter decomposition rates by altering leaf architecture or by reducing leaf quality, generating increased C:N ratios (Hartley 1998). To date, most studies of the effects of gall-forming insects on ecosystem processes have focused on temperate tree species, but much remains unknown about how galling insect species may modify ecosystem processes, especially litter decomposition, when they attack old-field herbaceous plant species.

Here we examine the interactions between a rosette gall midge (*Rhopalomyia solidaginis* Loew, Diptera: Cecidomyiidae) and a common old-field herbaceous

species (*Solidago altissima* L.) to determine if the galling herbivore alters plant architecture, leaf litter decomposition, and nitrogen (N) release. Previous studies have indicated that galling species on *S. altissima*, and *R. solidaginis* in particular, alter plant architecture and new ramet production of the host plant (Raman and Abrahamson 1995; Wise et al. 2006). In this study, we extend previous work on this study system (Crutsinger et al. 2006; Crawford et al. 2007) to explore the ecosystem-level consequences of the potential changes in host plant architecture and biomass that result from attack by *R. solidaginis*. Specifically, we ask: (1) What is the rate of galling at a study site in east Tennessee and what effects do galls have on plant architecture and aboveground biomass production? (2) Does galling affect leaf-litter quality and decrease litter decomposition and nutrient release?

Materials and methods

Study system

Solidago altissima (tall goldenrod) is a rhizomatous perennial that dominates old fields and roadsides throughout eastern North America (Werner et al. 1980; Semple and Cook 2006). In east Tennessee, *S. altissima* makes up, on average, 20% (range=5–47%) of the aboveground biomass in old-field ecosystems and also affects the dynamics and structure of the rest of the plant community (Souza et al., *in review*).

The insect fauna that attacks *S. altissima* is diverse and well studied at both the population and community level (Root and Cappuccino 1992; Root 1996; Abrahamson and Weiss 1997; Halverson et al. 2007). The rosette galling midge, *R. solidaginis*, is one of the most common galling species of *S. altissima* at our study site (Crutsinger, unpublished data). *R. solidaginis* has two generations per year in Tennessee. Emerging from over-wintering belowground in late April, the first-instar larvae begin feeding on nearby young *S. altissima* shoots and induce an inconspicuous, single-chambered gall in the apical meristem (McEvoy 1988; Wise et al. 2006). Short-lived adults emerge a few weeks later and females then oviposit in the apical meristems of goldenrod shoots, initiating a second generation of galls that often contain multiple chambers (2–12 chambers) (McEvoy 1988; Raman and Abrahamson 1995; Wise et al. 2006). Stem

elongation is halted at the site of the gall, but leaves are still produced, resulting in a rosette of leaves typically at the tip of the stem (Fig. 1). For this study, we focus on leaf litter collected after the formation of the second generation of galls. Adult midges emerge from the galls in the fall, and females oviposit in the soil where larvae hatch within 1–2 weeks and spend the winter underground, likely inside rhizomes (McEvoy 1988; Wise et al. 2006).

Study site

This study was conducted in a common garden experiment and various old fields located at Freel's Bend, which is part of the Oak Ridge National Laboratory National Environmental Research Park (NERP) near Oak Ridge, Tennessee (35°58' N, 84°17' W). The site has not been used for agriculture since 1943 and has been mowed annually. Soils at the site have a silty clay loam texture and are classified as Typic Hapludult. Mean annual rainfall is 1,322 mm and mean monthly temperature ranges from ~31°C (July) to ~3°C (January).

Gall prevalence and effects on plant architecture and biomass

To estimate rates of galling at our field site, in July of 2006 we randomly selected 25 *S. altissima* patches, ranging in size from 44 to 1,700 ramets per patch, within eight different old fields adjacent to our exper-

Fig. 1 Galled ramet (left) induced by attack by *Rhopalomyia solidaginis* on a *Solidago altissima* ramet. An ungalled ramet (right) is shown for comparison of the herbivore effect on plant architecture

imental garden. The fields ranged in size from 3,600 to 50,000 m². Within each patch, we tallied the proportion of ramets that were galled by *R. solidaginis*. Previous studies at the site indicate that neither patch size nor stem density affect rates of galling (Crawford et al. 2007). To quantify the effects of galling on *S. altissima* architecture and aboveground biomass production, we randomly selected a pair of *S. altissima* ramets within 20 of the patches. Each pair consisted of a galled ramet and its closest ungalled neighbor of similar size, likely of the same genet. We measured the height of each individual plant and then clipped each ramet at the soil surface. Green leaves from each ramet were removed, including the leaves from the gall, and estimated leaf area density, or leaf area per cm of stem, using a LI-3100C Area Meter (Li-Cor, Inc., Lincoln, NE). We used leaf area density as a measure of *R. solidaginis* induced leaf compaction. Aboveground biomass was then estimated for each ramet after oven-drying the tissue for 48 h at 60°C.

Galling effects on litter quality, decomposition and nutrient release

To quantify the effects of galling by *R. solidaginis* on *S. altissima* litter quality and to minimize environmental effects on plant litter, we collected senesced leaf litter from an established experimental garden of *S. altissima* in the autumn of 2005. The experimental garden was established in the previous spring and contained 42 1-m² patches of *S. altissima*, with each



patch containing one of 21 different genotypes collected from local *S. altissima* patches and grown in two replicate monocultures (see Crutsinger et al. 2006 for further details). Galled and ungalled litter from each of the 42 patches was randomly collected, air dried, homogenized within ungalled and galled litter type to minimize any potential differences among plants. Put another way, only leaf litter collected directly from galls is defined as “galled litter,” while ungalled litter from the stems of both galled and ungalled plants was considered “ungalled.” Subsamples were dried at 60°C for approximately 48 h to determine the oven dry mass. Subsamples were also ground to a fine powder using a Ball Mill Grinder (Cianflone 2601, Pittsburgh, PA), analyzed for total carbon (C) and nitrogen N using a Carlo-Erba Model 2500 CHN analyzer (Milan, Italy), and ashed at 550°C for 6 h. All data are shown on an ash-free oven dry mass basis.

To examine the effects of gall formation on rates of *S. altissima* leaf-litter decomposition and N release, we initiated a leaf-litter decomposition experiment over six months beginning in spring of 2006. Litter decomposition bags (10×10 cm) were constructed of a double layer of 0.8 mm polyester mesh on the top side and 0.2 mm (# 72191 polypropylene mesh) on the side in contact with the soil surface (Synthetic Industries, Atlanta, GA, USA). Bags were stitched together on three sides with polyester thread and, once filled with litter, were closed with stainless-steel staples. The larger mesh on the top of the bags allowed the mesofauna to colonize while the smaller mesh on the bottom prevented significant loss from fragmentation. Decomposition bags contained approximately 4 g of air-dried leaf litter (from either galled or ungalled litter), an amount that approximates the annual production of *Solidago* leaf litter per unit ground area occupied by a decomposition bag (i.e., 0.01 m²; Crutsinger unpublished data). We disassembled each rosette gall and homogenized litter from all galls prior to placing galled litter into decomposition bags to ensure that any potential differences in decomposition and nutrient dynamics are not a result of gall architecture and leaf compaction, but are the result of litter quality.

Decomposition bags were placed in an old field adjacent to the established experimental garden and were fixed to the soil surface using stainless steel nails. Bags were collected after 3, 6, 12, and 24 weeks in the field. An initial set of decomposition bags was transported to the field and returned to the laboratory

for analysis to determine loss in transit and initial mass. In total, the experiment consisted of 100 litterbags (2 treatments [galled vs. ungalled litter] \times 10 reps \times 5 collection dates). At each collection date, decomposition bags were returned to the laboratory in individual paper bags, air-dried, and hand sorted to remove materials that may have fallen or grown into the bags (e.g., seeds). Sorted litter was oven-dried at 60°C for 48 h, weighed, analyzed for C and N, and ashed (as above) to determine mass and nutrient loss.

Statistical analyses

We used separate paired *t*-tests to examine if the height and aboveground biomass differed between galled and ungalled ramets. We used a one-way ANOVA to compare differences in leaf area density in the galled portion of galled ramets, the ungalled portion of galled ramets, and ungalled ramets in our field observations. We examined if initial C and N concentrations or C:N ratios differed between galled and ungalled litter using separate *t*-tests. To examine if galling by *R. solidaginis* influenced mass loss or N release (determined as percent change from initial concentration), we used separate full factorial, fixed effects ANOVAs with litter type (galled or ungalled) and sample date as fixed effects in the model. Proportional mass and N loss data were arcsine square-root transformed in order to improve normality. For clarity, we present non-transformed data in the graphs.

We estimated decomposition rate constants (*k*) based on the negative slope from the exponential regression of the natural logarithm of the fractional ash-free dry mass remaining at each collection date for each individual set of replicate bags (Schlesinger and Hasey 1981; Weider and Lang 1982). To examine if *k* differed between galled and ungalled litter, we used a Wilcoxon's rank sum test. All statistical analyses were conducted with JMP 6.0 statistical software (SAS Institute, 2001, Pacific Grove, CA).

Results

Gall prevalence and effects on architecture and biomass

Rhopalomyia solidaginis attacked, on average, ~15% (range=3–35%) of all *S. altissima* ramets across 25

patches in eight fields at our study site. Furthermore, galling by *R. solidaginis* had substantial effects on *S. altissima* architecture and was positively related to total aboveground biomass. There was no difference between the height of galled and ungalled plants ($t=1.667$, $df=44$, $P=0.10$; Fig. 2a). However, galled ramets had ~60% greater aboveground biomass than ungalled ramets ($t=2.814$, $df=44$, $P=0.007$; Fig. 2b). In addition, *R. solidaginis* altered the architecture of *S. altissima*: leaf area density was four times greater on galled than on ungalled portions of stems ($F=34.086$, $df=2, 30$, $P<0.001$; Fig. 3). There was no difference in the leaf area density between the ungalled portion of galled ramets and ungalled ramets (Fig. 3).

Galling effects on litter quality, decomposition and nutrient release

Neither initial leaf-litter N concentration ($t=0.99$, $df=18$, $P=0.33$; Fig. 4b) nor C:N ratio ($t=0.045$, $df=18$, $P=0.96$; Fig. 4c) differed between galled and ungalled plants. However, initial leaf-litter C concentration was slightly higher (6%) in galled litter relative to ungalled litter ($t=2.29$, $df=18$, $P=0.03$, Fig. 4a).

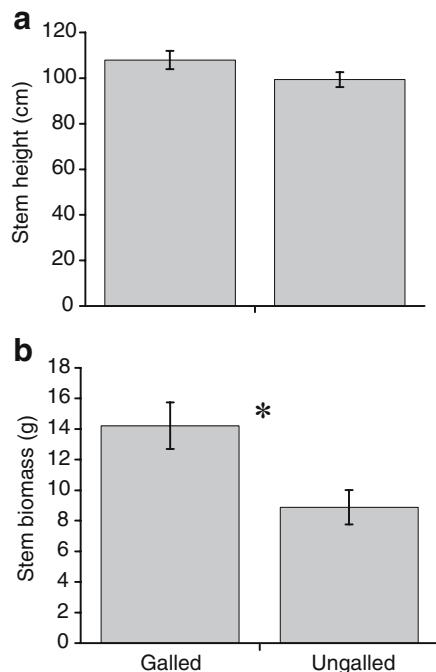


Fig. 2 Mean (± 1 SE) height (a) and aboveground biomass (b) of paired *Solidago altissima* ramets attacked by *Rhopalomyia solidaginis*. An asterisk indicates a significant difference between means at $\alpha=0.05$

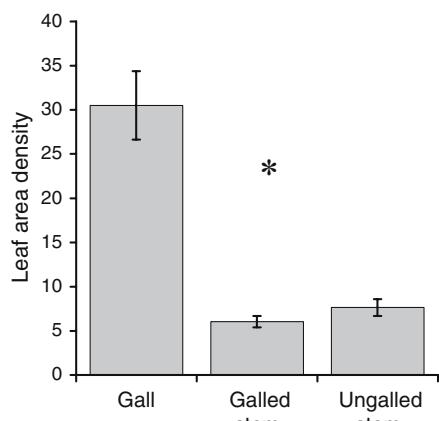


Fig. 3 Mean (± 1 SE) leaf area density (cm² of leaf area per cm stem) of the galled portion of *Solidago altissima* ramets, the ungalled portion of galled ramets, and of ungalled ramets, used to illustrate architectural changes in stems caused by *Rhopalomyia solidaginis*. An asterisk indicates a significant difference between means at $\alpha=0.05$. Using Tukey's HSD post hoc test, the density of leaf area of ungalled portion of galled ramets and ungalled ramets is not different

We found little effect of galling on leaf-litter quality and mass loss, but galling significantly impacted nutrient release patterns. Initially, mass loss was lower in galled litter than in ungalled litter, but this effect diminished after 12 weeks (Table 1, Fig. 5a). We found no effect of litter type (galled vs. ungalled) on k between galled ($k=0.48\pm 0.03$) and ungalled ($k=0.42\pm 0.01$) material ($Z=-1.389$, $P=0.16$). However, the proportion of N remaining was always higher in galled litter than in ungalled litter at each collection date (Table 1, Fig. 5b).

Discussion

Our results demonstrate that galling by *R. solidaginis* can be frequent, affecting up to a third of the ramets in at our study site, but rates of attack vary considerably (3–35%) among *S. altissima* patches. Such variation in galling rates was probably driven by underlying genetic variation in susceptibility of *S. altissima* clones among patches (Maddox and Root 1987; Wise et al. 2006; Crawford et al. 2007) and not by variation in soil nutrients or the spatial distribution of plants (Crawford et al. 2007).

Galled plants were not taller than ungalled plants, but they did have greater aboveground biomass.

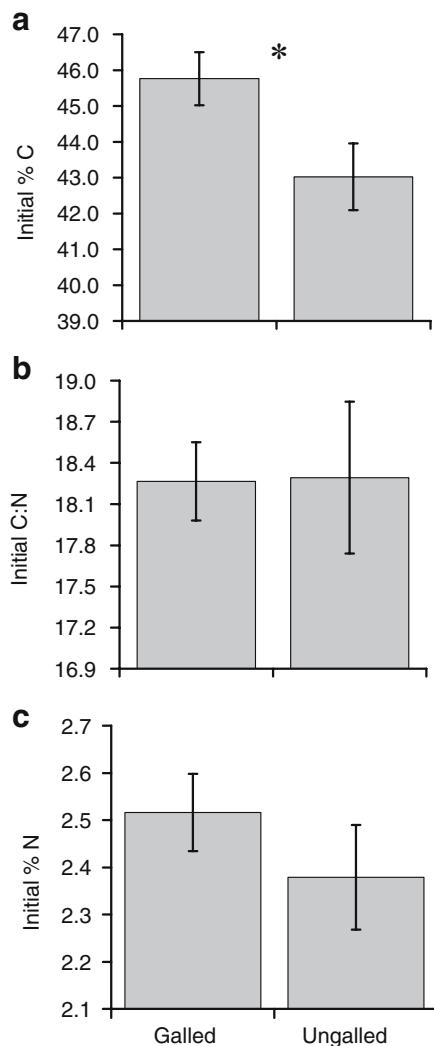


Fig. 4 Mean (± 1 SE) initial percent carbon (C) (a), nitrogen (N) (b), and C:N ratio (c) for galled and ungalled *Solidago altissima* leaf litter. Asterisks indicate a significant difference between means at $\alpha=0.05$

Galling insects often have negative impacts on the growth and reproductive output of *S. altissima* ramets (Abrahamson and Weiss 1997), and other studies have observed a reduction in stem growth of *S. altissima* when attacked by *R. solidaginis* (Wise et al. 2006). In this study, we failed to detect negative effects of galling on plant growth or fitness. In fact, stems with galls tended to have higher aboveground biomass than did stems without galls. There are two non-mutually exclusive hypotheses that may explain the apparent positive relationship between galling and aboveground biomass. First, it could be that higher aboveground biomass resulted from galling. Indeed,

Table 1 Full factorial, fixed effects ANOVA results for litter mass loss and nitrogen (N) remaining

| Variable | Factor | DF | MS | F | P |
|-----------|-------------------------------------|----|-------|---------|---------|
| Mass loss | Litter type (galled or ungalled) | 1 | 0.053 | 22.884 | <0.0001 |
| | Time | 3 | 0.353 | 164.721 | <0.0001 |
| | Litter type \times time | 3 | 0.023 | 10.850 | <0.0001 |
| | Error | 7 | | | |
| N loss | Litter type (galled or ungalled) | 1 | 0.085 | 8.274 | 0.005 |
| | Time | 3 | 0.280 | 27.195 | <0.0001 |
| | Litter type \times time | 3 | 0.012 | 1.220 | 0.309 |
| | Error | 7 | | | |

Wise et al. (2006) found that *S. altissima* plants can compensate for reduction in height caused by galls by changing resource allocation to new ramet growth, so that, for a given stem height, galled plants had greater new ramet production than undamaged ramets.

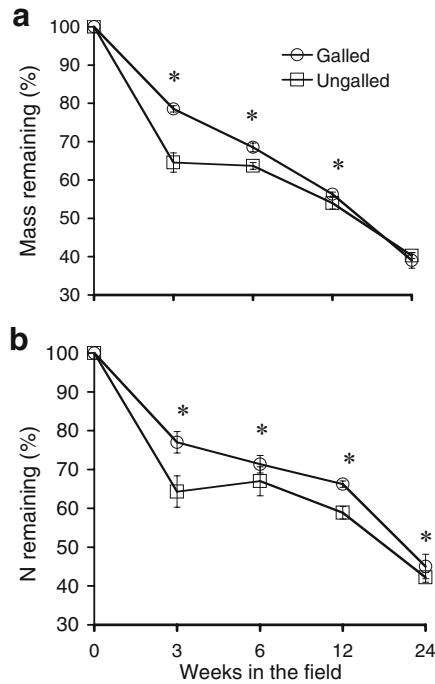


Fig. 5 Mean (± 1 SE) percent (a) mass remaining and (b) nitrogen (N) remaining in *Solidago altissima* leaf litter over 24 weeks. A line connects galled (circles) or ungalled (squares) treatments across time periods. Asterisks indicates a significant difference between means at $\alpha=0.05$ at a particular collection date

Another explanation is that *R. solidaginis* may attack larger and more vigorously growing ramets (Price 1991). A midge exclusion experiment would further clarify this issue. Nevertheless, the end result is that, for a given old field, there is likely to be more biomass input from galled *S. altissima* ramets than from ungalled ramets.

Gall effects on litter decomposition and nutrient release

Initial C concentration was higher in galled leaf litter and galled litter mass loss was reduced during decomposition, but mass-loss differences between galled and ungalled litter did not persist after 12 weeks or affect the overall rate of decomposition (k). Other studies have found that herbivore-induced changes in leaf chemistry can persist after senescence and have “afterlife effects” on decomposition and nutrient cycling (Choudhury 1988; Findlay et al. 1996; Schweitzer et al. 2005). For example, Findlay et al. (1996) found that decomposition rates were 50% slower in leaf litter of plants subjected to mite herbivory due to the formation of phenolic complexes. These molecules resist microbial degradation and tie up available N, effectively slowing decomposition and nutrient release (Palm and Sanchez 1991; Hattenschwiler and Vitousek 2000). While this may have also been a mechanism for the slowed N release patterns in galled litter, we did not measure defensive chemistry of *S. altissima* in response to galling by *R. solidaginis*. However, other studies have found that secondary chemistry in *S. altissima* can increase in response to other gall-inducing species (Abrahamson and Weiss 1986, 1997).

To date, most studies examining the role of galling herbivores on leaf-litter quality and ecosystem processes have focused on forest tree species (Findlay et al. 1996; Schweitzer et al. 2005). The mechanisms for changes in foliage quality after galling might be quite different for herbaceous species and have important effects on litter physical architecture (i.e., compactness, leaf toughness, etc.) and less on secondary chemistry, which could have substantially different effects on galled litter leaching and microbial utilization. Further research is needed to understand better how the response of *S. altissima* to herbivory affects other associated arthropods and mediates key ecosystem process, such as nutrient cycling.

Galling by *R. solidaginis* may also change the dynamics of litter inputs through the aggregation of leaves, which may have an important (although unmeasured) effect on rates of decay. Our study likely overestimated decomposition rate of galled litter because we disassembled the rosette galls prior to placing litter in the decomposition bags. Under more natural conditions, rosette galls would likely decompose more slowly than single leaves because the leaves in galls would be less exposed to the environment (due to the high aggregation of leaves), making them less susceptible to leaching, fractionation, and decomposer community colonization. However, because we were interested in understanding whether the potential effects of gall induction on litter chemistry affected decomposition, we did not estimate the rate of decomposition of intact rosette galls, as this would not allow us to differentiate between the effects of the physical structure of the gall versus the chemical quality of the galled litter. Intact rosette galls could also provide increased habitat diversity for microarthropods and other organisms (as they do aboveground, Crawford et al. 2007) thereby increasing rates of litter decomposition. It is unclear whether frass inputs from the arthropods associated with galls can affect nutrient dynamics in this study system, although we would likely see greater differences in initial chemistry if this were the case.

In conclusion, we found that *R. solidaginis* attacks up to a third of the individual stems of a dominant old-field plant species at our study site, and galling increases the architectural complexity of ramets. While there were modest differences between galled and ungalled initial litter chemical quality and mass loss, we did find significant differences in N release patterns. Future studies, in this and other species, could provide additional insights into the potential links between the effects of galling herbivores on herbaceous species and ecosystem processes. Given that *S. altissima* is abundant in old-fields throughout eastern North America (Semple and Cook 2006) where it can structure plant communities (Schmitz 2004; Souza et al., *in review*), litter inputs from galled *S. altissima* plants may be important in regulating old-field nutrient dynamics.

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